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Observations on plant development (IX)

The development of *Potentilla supina*

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The species is distributed over a wide area comprising, according to Hegi, the moderate and warmer climatic zones of Eurasia (in Europe it extends as far as Denmark and northern France). Hegi reports it to be an annual, biennial or perennial species, he characterizes this variability as follows: "the species is often annual, the root then perishes together with the main shoot in the autumn of the first year of life. If, for some reason the plant does not flower in the first year or did not die after the first florescence, it develops in autumn a many-leaved rosette which sets numerous axillary buds from which, in the following year flower stems develop". *P. supina* is a rather common species in Poland.

Sprouting was, in general, rapid and for further observation plants with an equal level of development were chosen.

The total investigations comprised seven series of experiments.

The plants were sown on the following dates in the course of the successive years:

I — Feb. 16, 1960; II — Aug. 28, 1961; III — May 18, 1962; IV — July 17, 1962; V — Sept. 27, 1962; VI — Apr. 6, 1963; VII — May 18, 1963.

The results are given separately for each experiment and in more detail for the exp. III—VII.

Experiment I — seeding time Feb. 16. Plants under continuous daylight (L_{24}) and short day (S_8) since March 20.

Plants of combination L_{24} ($n = 5$) — Earlier differentiation of leaves, rosette semi-erect, leaves distinctly larger.

Plants of combination S_8 ($n = 5$) — Spreading rosettes, leaves distinctly smaller differentiating later.

In the summer months flowering was only sporadically observed.

Part of the plants was transferred in autumn and kept until Dec. 28 in conditions of natural vernalization. Further observations were made up to the beginning of August.

Vernalization had the following effects:

1) the flowering of plants of combination S_8/vern./L_{24} and L_{24}/vern./L_{24} under L_{24} before and after vernalization was intensive and earlier,

Table 1

Differentiation of leaves and shoots

Experiment 1

Date of observation	Apr. 22		June 20		Aug. 20	
No. of days from sprout.	41		95		156	
Combination	L_{24}	S_8	L_{24}	S_8	L_{24}	S_8
No. of leaves	8.0	5.5	18.0	13.0	development of new leaves with simultaneous drying of old ones	older leaves still green
No. of lateral shoots	0	0	5.0	0		
Fresh weight					41.6	18.1

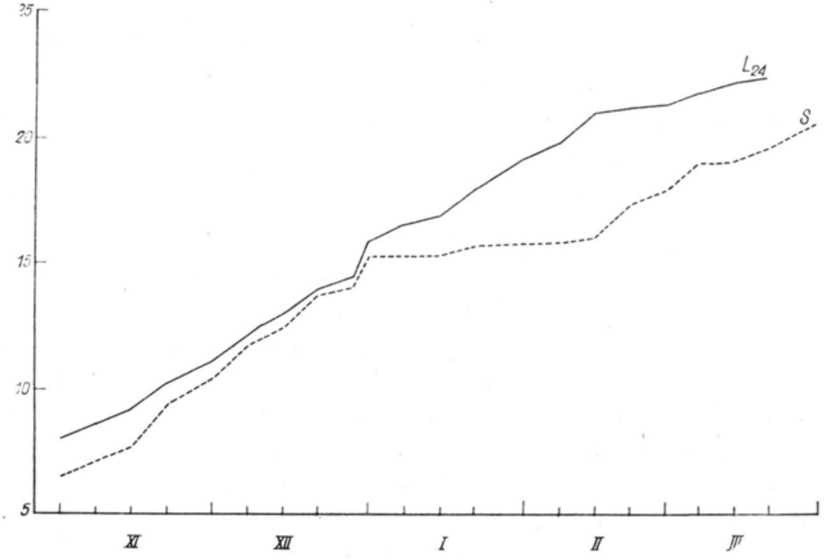
2) the plants of combination L_{24}/vern./S_8 and S_8/vern./S_8 also flowered, the latter however very poorly.

The S_8 controls did not flower and the L_{24} — only very poorly.

Experiment II — seeding time Aug. 28, vernalized between Nov. 19 and Dec. 27 (froze), and Dec. 31 and Jan. 20. They flowered in the beginning of May.

The number of leaves was counted on the plants of this experiment every week from the beginning of November to the end of March (Graph 1).

The number of leaves, thus the rate of differentiation, was somewhat higher under continuous daylight. The differences increased with rising



Graph. 1. *Potentilla supina*. Expt. II. Leaf number per plant

Calculation of leaf number increase, measurements at 7 days intervals; first calculated for plant aged 61 days (after 30 days of growth in different light conditions) light conditions. There were distinct differences (in favour of S_8) in the own age of leaves. The observations made in the preliminary experiments proved the effectiveness of vernalization and the inhibition of development under short day. The flowering of plants under continuous illumination without vernalization was poor, some of the plants did not flower at all. The behaviour of the control plants under long day varied from that observed in the subsequent experiments. This might have been due to the fact that in natural populations there occur forms with different "norms" of reaction in respect to the "need" of vernalization.

The seeds for the following experiments were collected from plants of exp. II. The tests were carried out with a relatively large number of plants and in more combinations.

Experiment III — seeding time May 18, 1962 (sprouting May 25).

Table 2

Observations on vegetative development

Date of observ.	No. of days from sprout	Charecteristics	N	L_{16}	S_8
		Habitus: rosette arrangement	erect	horizontal	horizontal
		Leaf size	long petioles largest blades	medium	smallest blades short petioles
7.VII	43	Lifetime of 1 pair of leaves			
		dry	59 %	8.0 %	9 %
		yellow	38 %	5.5 %	21 %
		green	2 %	86.5 %	71 %
7.VII	43	No. of rosette leaves	8.0	8.9	8.3
17.VII	53		8.8	10.8	11.0
			rapid development of axillary buds into foliated shoots	axillary buds develop v.slowly, only in some of the plants short stems with several leaves formed	axillary buds develop v.slowly into primordia of shoots which slowly differentiate leaves
17.VII	53	Total no. of leaves and shoots (resp.shoot primordia)	25.0	41.3	42.3
24.VII	66		48.5	42.4	43.2
14.VIII	81		128.0	54.5	66.3
7.VII	43	Fresh weight and % of dry weight	-	0.76 13.1 %	0.35 14.0 %
24.VII	66		4.75 16.8 %	3.9 15.4 %	2.5 16.0 %
14.VIII	81		19.8 21.0 %	10.6 16.7 %	9.4 15.8 %
30.VIII	97		- -	12.4 18.5 %	11.9 16.1 %
11.IX	109		- -	11.4 18.4 %	10.4 15.4 %

On June 10 the plants were placed under three different illumination systems:

N — varying natural daylight,

L_{16} — 8-hours natural daylight + 8 hrs in growth chamber fluorescent tube 3500 Lux,

S — short (8-hr) natural daylight.

Since autumn the plants of combinations L_{16} and S_8 grew in the growth chamber, and those of combination N in the glasshouse. On August 1 part of the plants of combinations L_{16} and S_8 were transferred to natural daylight.

The plants of combination N, L_{16}/N and S/N (though the latter obviously with some delay) rapidly developed shoots which in full summer were longer and procumbent, in the later part of summer — shorter and more densely foliated (see Photo 1). Soon buds formed on the stems and the plants came into flower (see Table 2 and 3).

Table 3

% of flowering plants

Experiment II

Date	No.of days from sprout.	N	L_8/N since Aug.1	S/N since Aug.1	L_{16}	S
17.VII	53	80% flowered				
1.VIII	67	100% flowered flower. profuse				
30.VIII	97	Overblowing, dying of leaves and shoots. Part of the plants died, part developed new rosettes from axillary buds	medium intensity floresc.		low intens. floresc.	
6.IX	105		24% flowered	50% flowered	5.7% flowered	veget
15.IX	114		30	78	6.4	
27.IX	125		41	80	7.0	
1.XI	159		overblown		sporadically new flowers still come into bloom	

In the plants of combination S_8 — which did not flower before winter — the development of the "shoots" did not advance beyond the primordial stage.

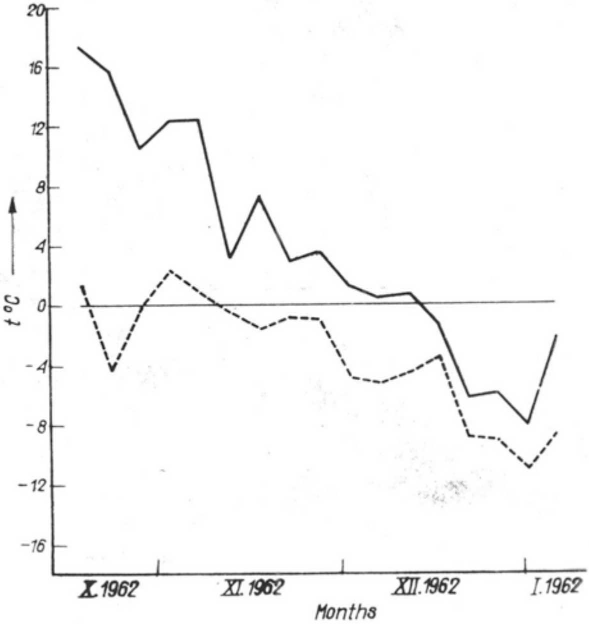
In the L_{16} plants, very short stems, remaining vegetative until late autumn, developed from the bud primordia with great delay; in some

Photo 1. *Potentilla supina*, L_8, Expt. III, 20.IX.1962

Photo 2. *Potentilla supina*, N; Expt. III, 20.IX.1962

cases the shoot primordia extended somewhat, each forming one flower bud (see Photo 2).

In late autumn most of the "summer" rosette leaves gradually died and the slow development of new rosettes started. During autumn and winter exlusively vegetative growth occurred slowed down till January, then gradually accelerated. There were no differences in the development and growth of the plants of combination N, therefore in further observations only one result will be given for all N combinations. Part of the plants of combinations L_{16} and S_8 were submitted at the age of



Graph. 2. Mean temperature max. and min. during the vernalization period in expts III and IV

Table 5

Speeding up of development as the result of vernalization in no. of days as compared with L_{16} and N

In relation to:	$L_{16}/v/L_{16}$		$S/v/L_{16}$		$L_{16}/v/S$		$S/v/S$	
	a	b	a	b	a	b	a	b
L_{16}	148	148	139	148	114	114	114	114
N	177	177	170	177	143	143	143	143

a - in relation to maximum no. of plants with shoots.

b - in relation to ± 50% flowering plants.

Table 4

Observations on development of vernalized and non-vernalized plants (20-35 plants in combinations)

Date of observation	No. of days		No. of plants with shoots (a) and No. of flowering plants				Daylength before vernal.				Daylength after vernal.				S_8
	from sprout.	from end of vernal.	N		L_{16}		$L_{16}/v/L_{16}$		$S_8/v/L_{16}$		$L_{16}/v/S_8$		$S_8/v/S_8$		
			a	b	a	b	a	b	a	b	a	b	a	b	
8.II	259	34	0	-	0	-	100	65	85	50	67	0	75	0	
15.II	266	41	0		0		100	75	100	65	67	0	75	7	
22.II	273	48	0		0		100	90	100	75	90	30	80	15	
12.III	293	68	0		0			100		90	100	40	100	50	
4.VI	377	-	0		30	0									
14.VI	387	-	0		45	0									
27.VI	400	-	0		80	30									
4.VII	407	-	0		94	80									
10.VII	413	-	17	0	100	90									
18.VII	421	-	25	0											
2.VIII	436	-	70	50	100	100									rosettes exclusively

The date of coming into flower in comb. N and L_{16} did not change in dependence on whether the given plants flowered in the preceding year or not.

138 days to the influence of natural vernalization for 87 days in the period from Oct. 10 to Jan. 5.

The temperature variations in the course of vernalization are shown in Graph 2.

As shown by the Tables 4 and 5 the speeding up (in number of days) of development by vernalization was considerable, as compared to that in combinations L_{16} and N. The control plants only formed rosettes, thus vernalization was found to abolish in a large extent the inhibitory influence of short day.

Experiment IV — seeding time July 17, 1962, sprouted on July 30.

The daylength was differentiated on August 26. Observations were made on the following combinations:

1) controls under natural varying daylight (N) transferred to glasshouse in autumn;

2) plants under short (8-hr) day (S_8);

3) plants under 16-hr day (growth chambers), from May 1 natural daylength, kept in glasshouse;

4) part of the plants combination N were placed on May 1 under continuous daylight (natural + illumination with fluorescent tubes of 3500 Lux during night).

On Oct. 10 some of the plants of combinations N, L_{16} and S_8 were transferred to conditions of natural vernalization (age of plants 72 days). Vernalization lasted 87 days (to Jan. 5), not one plant died (Graph 2).

After vernalization each combination was separated into two groups: one was placed under 16-hr and the other under 8-hr daylight. Thus

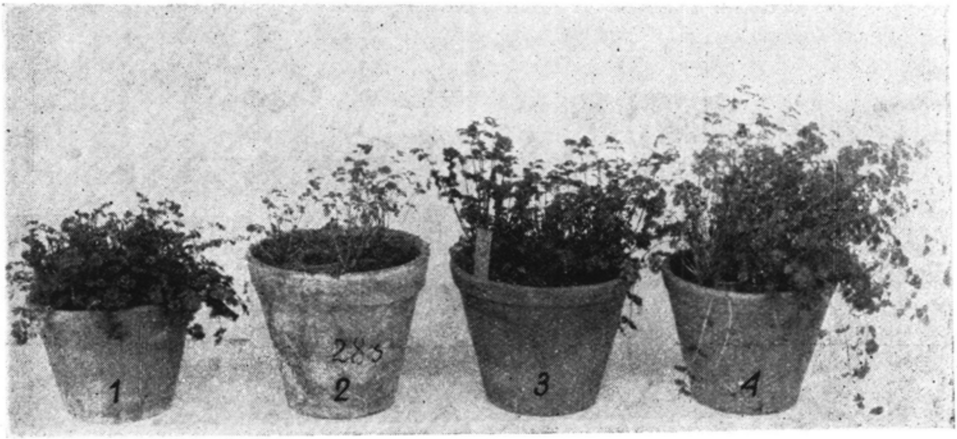


Photo 3. *Potentilla supina*, Expt. IV, 22.I.1962

1 — N; *2* — S_8; *3* — L_{24}; *4* — L_{16}

Table 6

Generative development in the particular combination

Experiment IV

Date of observ.	No. of days		N		N-L_{24}		L_{16}		L_{16}/v/L_{16}		N/v/L_{16}		S/v/L_{16}		L_{16}/v/S		N/v/S		S/v/S		S	
	from sprout.	from end of vernal.	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
8.II	193	34	0		0		0		100	36	100	21	90	23	60	0	90	0	35	0		
15.II	200	41	0		0		0		100	40	100	35	95	40	68	0	95	0	70	0		
4.III	217	58	0		0		0		100	50	100	50	95	50	86	0	95	0	70	0		
12.III	225	66	0		0		0		100	67	100	63	95	60	95	0	100	12	70	8		
7.III	231	71	0		0		0		100	90	100	100	100	60	95	11	100	30	70	10		
1.V	244	85	0		0		0						100	80	95	15	100	45	75	25		
15.V	289	-	0		64	-	0															
22.V	296	-	0		77	70	0															
4.VI	309	-	0		100	90	50	0														
8.VI	313	-	0		100	100*	83	35														
17.VI	319	-	0				100	45														
27.VII	332	-	8	4			100	100														
10.VII	345	-	24	16																		
18.VII	353	-	57	30																		
2.VIII	367	-	84	77																	rosettes exclusively	

a - % of plants with shoots.

b - % of floresc. plants.

*They chiefly flower on lateral shoots, however, in part of the plants the apex trasforms into a stem and flowers.

the following combinations were obtained: (5) L_{16}/vern./L_{16}, (6) N/vern./L_{16}, (7) S_8/vern./L_{16}, (8) L_{16}/vern./S_8, (9) N/vern./S_8, (10) S_8/vern./S_8.

Table 7

Speeding up of development as the results of vernalization in no of days in relation to controls L_{16} and control N - day

Experiment IV

In relation to	L_{16}/v/L_{16}		N/v/L_{16}		S/v/L_{16}		L_{16}/v/S		N/v/S		S/v/S	
	a	b	a	b	a	b	a	b	a	b	a	b
L_{16}	126	102	126	102	102	102	94	69*	75	75	69	69
N	174	150	174	150	150	150	142	101*	142	122	123	109

Compared: a - ca 100 % with shoots.

b - ca 50 % with flowers.

*Being an exception where the percentage is lowered.

The number of plants in the particular combinations was 25—75 (except the control combination L_{16}, n = 6). In the vegetative period 7.5 per cent of the plants of combination N and 11 per cent of combination L_{16} came into flower from the end of August to the end of September (as shown by Photo 2).

The flowers overblew rapidly, up to mid October they were all past flowering.

The observations on the generative development in the particular combinations are compiled in Table 6.

The speeding up resulting from vernalization is shown below in Table 7. For the habitus of the plants see Photo 3 (of January 22).

Table 8

The length of the shoots in the particular combinations in dependence on ilumination conditions

Experiment IV

Date of observ.	No. of days from sprout.	L_{16}/v/L_{16}		N/v/L_{16}		S/v/L_{16}		L_{16}/v/S		N/v/S		S/v/S	
		a	b	a	b	a	b	a	b	a	b	a	b
22.II	207	9,8	16,2	8,6	15,8	2,5	15,2	4,1	-	5,0	-	5,7	-
12.III	225		26,4		26,1		22,5	5,5	-	5,0	11,0	4,5	8,7

a - mean length of shoots without buds in cm.

b - mean length of flowering stems in cm.

The length of the shoots in the particular combinations vernalized was different, thus expressing different growth rates in the combinations, in dependence on the illumination conditions (Table 8).

Table 9

The lengths of shoots in different combinations

Experiment V

Date of observ.	No. of days		N		N-L_{24}		L_{16}		L_{16}/v/L_{24}		L_{24}/v/L_{24}		N/v/L_{24}		S/v/L_{24}		L_{16}/v/L_{16}		L_{24}/v/L_{16}		N/v/L_{16}		S/v/L_{16}		L_{16}/v/S		L_{24}/v/S		N/v/S		S/v/S		S	
	from germ.	from end of vernal.	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
25.II	142				10	0																												
10.III	155	10			25	12	-	-	10	0	12	0	50	0	45	0																		
15.III	160	15							20	0	56	0	70	0	80	15																		
20.III	165	20																																
1.IV	176	31			30	25			35	5	75	16	95	16	80	15																		
23.IV	199	54							50	30	75	60	95	88	85	65																		
3.V	209	64							60	40	84	75	100	92	90	75																		
25.V	231	86			70	30																												
4.VI	241	96																	8.5	0														
8.VI	245	100			100	80																												
13.VI	250	105	14	0			5	0											17	14			2.5	2.5										
20.VI	258	113	33	24	100	100	20	0									9	0	17	17	23.5	6	5.0	2.5										
27.VI	264	119	33	24			20	10									20	6	36	20	47	9	15	2.5										
4.VII	271	126	43	30			65	30									30	12	80	34	61	32	35	15										
9.VII	276	131	43	30			75	50									65	35	90	75	80	65	80	40										
18.VII	285	140	60	50			85	60									85	40	100	84	88	74	100	40										
2.VIII	300	155																							20	0			8	0				
6.VIII	304	159	70	50																							16	0			12.5	3		
18.VIII	316	171																									23	16			12.5	6		
19.IX	343	198																											15	15	20	13		
20.IX	349	204																							25	20	30	23	23	23	20	20		
2.X	361	216																							30	30	40	23	30	30	22	22	3	0

a - % of plants with shoots.

b - % of flowering plants.

The fresh ad dry weight were highest in plants growing under 16-hour day, and, after vernalization, under short day.

Experiment V — seeding time Sept. 1962, sprouted on Oct. 6. Placed under different daylengths on Oct. 29 (23 days after sprouting).

The experiments were performed in the following combinations:

1) controls — natural varying daylight (N) in glasshouse,

2) short day (S_8),

3) 16-hr day (growth chamber — 3500 Lux). Since May 1 in glasshouse under natural daylight,

4) up to Dec. 12 like N then L_{24} (growth chamber).

Natural vernalization from Jan. 28—Feb. 28 (plants submitted to vernalization at the age of 114 days, duration 31 days (Graph 4). After vernalization the plants were separated into the following groups:

(5) L_{24}/vern./L_{24}, (6) L_{16}/vern./L_{24}, (7) N/vern./L_{24}, (8) S_8/vern./L_{24}, (9) L_{16}/vern./L_{16}, (10) L_{24}/vern./L_{16}, (11) N/vern./L_{16}, (12) S_8/vern./L_{16}, (13) L_{16}/vern./S_8, (14) L_{24}/vern./S_8, (15) N/vern./S_8, (16) S_8/vern./S_8.

Number of plants in each combination 13—40, from 15.V. the plants were transferred to natural daylight plus complementary artificial light.

Observations on generative development are compiled in Table 9.

As seen from the tables, vernalization gave, in contrast to expt. III and IV, no accelerating effect as regards generative development.

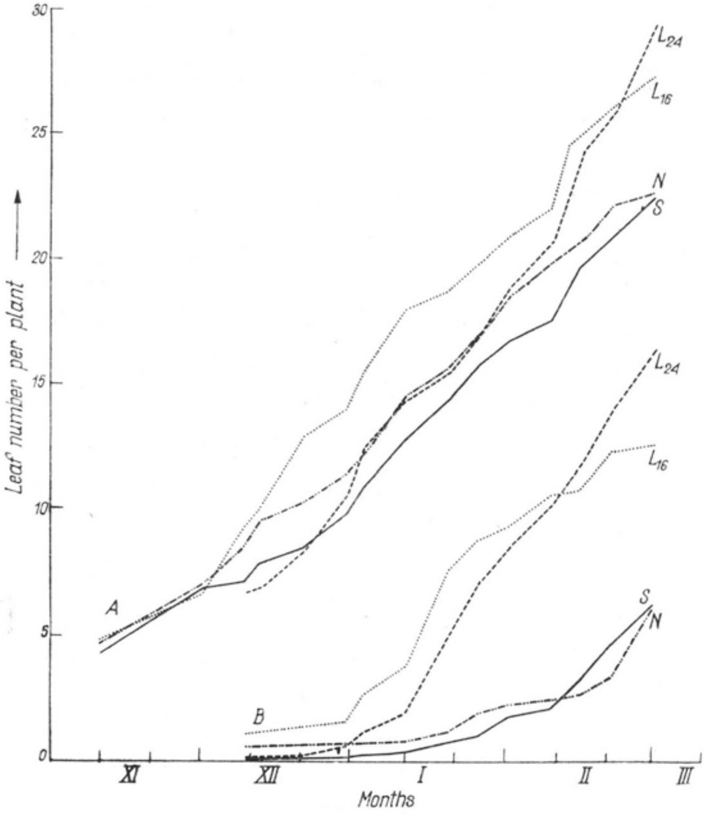
The vernalized plants of combination L_{24} began to pass into the generative phase at about the same period as in the previous experiment, only the uniformity within the experimental population was somewhat better, thus probably causing a certain small general acceleration.

The plants which grew under short day before vernalization exhibited somewhat quicker development.

Those which grew under 16-hr light after vernalization, flowered at the same time as the controls.

Plants growing after vernalization under short day passed into the generative phase with great delay, as compared with the N combination (average 103 days, comparing similar frequencies of flowering plants). On the other hand, vernalization had a positive effect on plants growing under short day, enabling them to pass into the generative phase, the differences in the light conditions before vernalization remaining in this case without effect. In the non-vernalized combination, in order to determine the increment of the leaf mass, the number of leaves and side shoots (or respective primordia) was counted in the period Nov. 10 — March 1. The results are illustrated by the Graph. 3.

Seeding in the last two experiments fell to the period of what is considered as optimum light conditions (exp. VI on Apr. 6, 1963 and exp. VII on May 18, 1963. These two experiments were made additionally



Graph. 3. Number of leaves and side shoots was counted in the period Nov. 10 — March 1

A — total leaf number; *B* — number of dead leaves

to verify whether, if seeded at these dates, the plants (as observed in exp. III) would pass earliest into the generative phase, whether florescence would be most intensive and the apex would develop into a stem and flowers, and what is the relation between all this and the survival of the plants. The plants might namely, in view of such a character of development, behave like a monocylic annual biotype.

Experiment VI — seeding time Apr. 6 in glasshouse under natural daylight. The observations are listed in Table 10. Number of plants 100.

Table 10

Generative development of plants

Experiment V

Date of observ.	Number of days from sprouting	Observations
May 26	44	Plants develop shoots in 80%
June 5	54	Florescence of plants 100%. No. of shoots on one plant 15 - 22. Intensive yellowing of rosette leaves
June 21	70	Apex grows into shoot. Main stems flower. Rosette leaves almost dead
Aug. 2	112	Partial overblowing and drying of leaves on shoots, part of the shoots die
Aug. 13	123	Axillary buds on the lower part of shoots and axillary buds develop extending into new shoots which soon set buds
Sept. 12	152	First shoots died, further development from axillary buds

Experiment VII — seeding time May 18. The experiments were made in combinations with 40 plants in each:

Table 11

Generative development of plants

Experiment VI

Date of observ.	No.of days from sprouting	N			L_{24}			L_{24sh}			L_{16}			L_{16sh}		
		a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
July 5	41	40	0	0	100	100	100	100	85	85	95	40	0	35	0	0
10	46	87	30	10					100	100	100	90	75	45	20	80
19	55	100	57	75								100	100	100	90	100

a - % of plants with shoots.

b - % of flowering plants.

c - % of plants in which apex developed into shoot.

1) controls growing under varying natural (N) daylight,
2) L_{24} — continuous natural daylight + fluorescent light of 3500 Lux,
3) L_{24Sh} — as above, plants shaded (light intensity reduced by 50%),

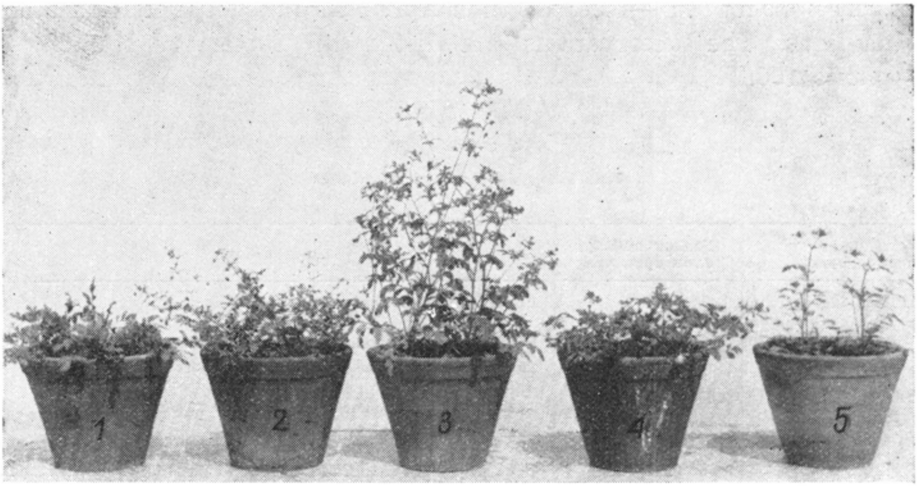


Photo 4. *Potentilla supina*, Expt. VII, 20.VII.1963

1 — control; *2* — L_{24}; *3* — L_{24Sh}; *4* — L_{16}; *5* — L_{16Sh}

4) L_{16} — 16-hr daylight,

5) L_{16Sh} — the same shaded with cheesecloth.

Data on generative development are compiled in Table 11.

The plants of the individual combinations differed distinctly as regards their general habitus (Photo 4):

N — rosette arrangement, shoots growing horizontally or somewhat slanting. Main stem backward in development as compared to the side shoots.

L_{24} — semi-erect arrangement. Main stem branched, developed equally to, or more than lateral shoots. Leaves smallest of all combinations.

L_{24Sh} — erect arrangement. Main stem develops quicker than lateral shoots.

L_{16} — arrangement rather rosette-like, lateral shoots slanting in respect to horizontal ones.

L_{16Sh} — erect arrangement. Main stem more developed than lateral ones. Leaves largest of all combinations.

Below some of the indexes of vegetative development are compiled (Table 12).

Towards the end of September:

N — "summer shoots" have overblown, intensive development of new shoots from auxiliary buds occurs.

L_{24} — summer shoots died, new ones develop from axillary buds. L_{24Sh} — about 40 per cent of plants died, the remaining ones develop from axillary buds,

Table 12

Generative development of plants

Experiment VII

Generative development	Date of observ.	No. of days	N	L_{24}	L_{24sh}	L_{16}	L_{16sh}
No. of leaves in rosette	July 5	41	6.7	9.1	9.9	8.9	7.2
No. of green leaves in rosette and on main shoot	July 21	57	5.6	12.1	15.2	7.7	-
No. of side shoots	July 5	41	1.9	4.1	2.2	2.6	0.5
	July 10	55	4.9	5.0	2.9	5.0	2.6
Fresh weight	July 5	41	3.0	4.8	5.3	3.9	4.7
	July 25	61	4.3	3.7	4.7	5.9	3.8
	Aug. 3	69		3.1	2.6	3.7	1.2
Percentage of dry weight	July 5	41	21%	23%	20%	20%	15%
	July 25	61	21%	24%	23%	21%	20%
State of rosette leaves	July 23	59	green or partly yellowed	drying or dry	dry	beginning to yellow	beginning to dry

L_{16} — about 50 per cent of buds died, the remaining ones develop from axillary or lowest axillary buds of shoots.

L_{16Sh} — all plants, after the death of their shoots, develop from axillary buds of the lowest axillary buds on old shoots.

RESULTS AND DISCUSSION

1. In many rosette-plants the beginning of generative differentiation concurs with the phase of stem formation. As inducing agents act: the day-night ratio or lowered temperature or else both these influences together, causing the extension of the apex into a stem and florescence.

In other plants the main apex differentiates further vegetatively, whereas an indication of generative induction may be found in the setting and development of axillary buds (Thomas 1962). Ryńska (1962), when examining native white clover, established that the setting of lateral buds is even speeded up by short day conditions, however, their further growth is inhibited.

P. supina forms a rosette, the development of which can be measured by the number of differentiating leaves. It is accelerated under continuous illumination retarded under short day, and also shows a positive dependence on light intensity (Graphs 1 and 3).

The plants set axillary buds as primordia of lateral shoots. Under short day their extension growth is strongly inhibited. On the other hand, under continuous and long day, if a certain limiting value of light intensity is exceeded, or if short day interacts with vernalization, the primordia develop into generative shoots elongating at the tip and often forming branchings of the 2-nd order.

This type of development prevailed in our experiments.

1. However, in conditions more and more removed from the optimum for generative processes, only single flowers developed on shortened and unbranched shoots and the plants overblew quickly (Photo 2).

This type of flowering was observed in plants of the L_{16} combination in expt. III, and in combination N of exp. IV when the plants came into flower in late summer.

In the majority of cases, even when the lateral shoots were well developed and flowered profusely, the main apex remained in the vegetative phase differentiating only further rosette leaves.

Only in optimal conditions activating generative development as in expt. VI and VII, and, sporadically, in combinations NL_{24} of expt. IV, a transition of the main apex to the generative phase was observed with a varying ratio of the growth rate of the main stem to that of the lateral shoots.

It is in these conditions that the own age of the rosette leaves was shortest.

The question arises, whether the transition o fthe apex to a flowering stem leads to the death of the plant. Observations of the plants of expt. VI and VII proved that the monocyclic type of development was correlated only in a certain percentage of plants with their death.

In most cases, in the phase of wilting of the main stem and after drying up of the rosette leaves, the axillary buds and the axillary buds in the lowest axils of the dead leaves of the main stem began to develop. These shoots rapidly extended into stems and came into flower. *P. supina* behaves also in these conditions like a polycyclic plant and the death of the entire plant after the first life cycle would only be an extreme modification.

2. The light conditions and in the first place daylength are the chief regulator of the processes of flowering, whereas light intensity ranks second (particularly when in interaction with long day). Probably changes in the spectral composition of light play some role here.

Thus, within the annual cycle of variation of light conditions, those prevailing in this country in the first half of summer are optimal as regards generative processes.

Observations on plants of the control combination (N) in the annual cycle indicate the varying activity of plants both as regards growth and vegetative differentiation processes, as well as flowering.

In plants seeded in the optimum period (mid April — end of May) the most rapid initial growth was observed and the highest intensity of generative processes: rapid development of lateral shoots, full bloom within 40—55 days from germination, the greatest uniformity in coming into flower, profuse florescence and frequent development of the apex into a stem.

In the second half of September (also in glasshouse conditions) the plants ceased to flower (so did those sown in the post-optimum period as in expt. IV or growing previously in less favourable conditions of light intensity as L_{16}, expt. III). At the same time the "summer leaves" began to dry and the growth of shoots slowed down. The process of partial dying, with a diminishing rate of development of new leaves and flower buds, becomes gradually more and more intensive (October). In the period of what is called "minimum life conditions" (October-December) the plants pass through a phase of "minimum activity" lasting to mid January. The second part of winter and early spring (lower part of curve of rising light conditions in annual cycle) are characterized by an acceleration and gradual intensification of the processes of leaf differentiation and growth (see Graphs 1 and 3). The shoots develop progressively and come into flower.

It is interesting that the time of flowering was the same for all plants of combination N, whether for those of expt. III flowering a second time of for the majority of plants of exp. IV and all those of exp. V flowering for the first time. The period of florescence of the particular plants in one experiment ranged from the end of the first ten days of July to the beginning of August, thus, from the point of view of light conditions, it was post-optimal (varying only in a smaller degree for combination L_{16}, and in a larger — for L_{24}). It should be borne in mind that this is true of plants which spent the whole winter in the glasshouse or growth chambers and grew vegetatively for a long time.

These facts might be interpreted in the light of various hypotheses, namely:

a) recurrence of the juvenile phase, in the sense that new rosettes developing from the axillary buds of plants generatively "mature" required a certain time to go through the juvenile phase and only then passed into the phase of generative induction;

b) the often stressed inhibitory effect of young growing leaves on generative processes. This influence subsides only with their ageing (Lang, 1956 and references quoted therein especially De Zeuw);

c) the fact that this inhibitory influence of leaves would be still stronger, since they had partly developed under conditions of relatively short day. According to the observations of Alleweldt (1963) on *Vitis* this inhibitory influence is "reduced" in this plant only when the ratio of the surface areas of long- to short-day leaves exceeds 2.5:1, thus inhibition occurs very slowly.

We may omit the first hypothesis as least probable, but the phenomena described under (b) and (c) may and certainly do occur.

This would also explain the fact of the earlier flowering of the plants of exp. VI and VII, the vegetative phase of which lasted a much shorter time, and which had a rosette of low-weight leaves and aged rapidly.

The acceleration of development observed in combinations L_{16} and L_{24}, in spite of the relatively low light intensity seems to speak for the third and perhaps partly for the second hypothesis, since the process of leaf ageing, particularly in combination L_{24} was distinctly quicker.

3. Light intensity, as results from the reaction of plants of combinations N, L_{16} and L_{24} exerts a strong influence on the entire process of flowering including also the growth of stems. Mathon 1960 and coworkers gave many very interesting facts about the change in photoperiodic responses types in plants according to variations of light intensity and quality (Mathon 1963; Mathon, Stroun, Grossin, Gaillochet, Gandrieu 1962; Mathon et Stroun 1962). In our experiments the interaction of this influence with the quantity of light is stronger in expt. IV and V than for instance in VII.

Generative development, in combinations L_{16} and L_{24} of exp. IV, as compared with that in the same combinations of exp. V occurs by about 30 days earlier (the difference would have been still wider if the L_{24} controls had remained the whole time under continuous illumination). For the vernalized combinations of expt. V the same difference amounted to 80 days, whereas for the plants of expt. VII developing under optimum light conditions whether shaded or not the differences were relatively very small. As far as the influence of daylength on the development of flower organs and the process of florescence is concerned *P. supina* reacts strongly to long daylight, flowering earlier and more intensively when the photoperiod is changed from 16 hrs to continuous illumination.

Under short day the plants do not come into flower, or the shoots develop very late and only sporadically (expt. V, 460 days after germination).

Whereas in many hibernating annual plants with a distinct reaction to long photoperiods generative development was observed also under the joint action of short day and light intensity, in *P. supina* no changes of this type were noted. The inhibitory effect of short day was equally strong in various seasons.

If, however, the moment of setting of shoot primordia is assumed as the morphological index of what is called "generative induction", then *P. supina* should be considered as a photoperiodically neutral species, highly sensitive to the inhibitory influence of short day on the development of lateral shoots, and in this way, on the differentiation of the generative organs proper. This point of view seems closer to truth, therefore *P. supina* should be considered as a "neutral" plant, as regards the phase of generative induction, and as a distinctly long-day plant as far as the subsequent development and growth phases of formation of generative organs are concerned.

This inhibitory influence of short photoperiod seems to be relatively independent of light intensity, since it could be observed in plants sown at various dates and growing under conditions of elevated temperature.

4. Exposure of the experimental plants in the autumn—winter period to the action of low temperature (natural vernalization) produced in most cases a distinct speeding up of generative development in long-day combinations, on the other hand, in the "non-inductive" conditions of short day, at least part of the plants passed into the generative phase.

Vernalization acts here as an agent "compensating" the light conditions non optimal for the development of the plant.

The effect of vernalization measured by the number of days by which the florescence was speeded up in comparison to the control combinations was strongeset in expt. III, a little weaker but still quite strong in expt. IV (Tables 5, 7), whereas in expt. V, quite unexpectedly, it was distinct only in the case of short photoperiod combinations (Table 9).

To date a certain number of instances has been described in which vernalization played the role of a facultative developmental factor.

In the wild *Trifolium repens*, Haggar (1961) observed upon vernalization a general intensification of vegetative and generative development, the effect of vernalization decreasing from "January" that is at the moment when the photoperiodic conditions change from waning to rising.

Arabidopsis thalliana, when growing under lower light intensity, reacted positively to vernalization and the plants came into flower (Napp-Zinn 1962).

This interrelation between the effect of vernalization and light intensity was observed by Wellensiek (1960) in *Campanula medium*: he found that in autumn the required minimum of vernalization days and of the plant's age, making possible its flowering under short day, had to be higher than when the experiment was made in early spring.

Kurth (1955) reports the intensifying effect of vernalization on development for the following plants: *Vicia villosa* and *V. sativa*, *Sinapis* and *Agrostemma*, the influence of vernalization increasing with waning daylight. Büttner (1960) observed the efect in *Lathyrus*.

Raphanus sativus (Tashima, cit. Lang 1956) comes into flower without vernalization under continuous illumination, and, when vernalized — also under short day, so does *Melilotus albus* (Kasperbauer et al. 1962), whereas *Campanula medium* (Wellensiek 1960) flowered under long and short day after longer vernalization but when the treatment was short, the plant flowered only under long day.

Generative induction in *Trifolium subterraneum* (Evans 1950) in conditions of waning daylength could only be demonstrated in interaction with lowered temperature. Winter wheat after long vernalization forms ears under short day as well, similarly as a number of spring wheats (Razumov and Oleynikova 1960). The positive joint action of vernalization and short day, making possible generative development, was also observed on *Centaurium umbellatum* (Listowski and Jeśmanowicz 1962).

It may be added here that, as observed frequently by the authors in experiments with other plants and reported by Haggar (1961), even when vernalization speeds up or induces florescence in conditions considered as non-inductive, nevertheless the intensity of the process of florescence is always higher in plants growing under normal summer daylight.

Lang (1956), on the basis of observations on spinach and *Raphanus*, believes that vernalization reduces the critical daylength required for flowering, and this reduction may go so far that the plant behaves like a photoperiodically neutral species.

A lot of very interesting observations brought Mathon (1960), Grossin et Mathon (1961) and Gandrieu, Mathon, Grossin (1962). A change in types of the photoperiodic responses was observed in interaction with vernalization. Very often the critical length of the day lay by more shortened day after vernalization.

It should be added to the statement of Lang that vernalization "reduces" the light intensity minimum at which the process of flowering can take place.

In reference to the above mentioned behaviour of *P. supina*, it will be of interest to discuss several alternative solutions explaining the influence of light conditions in interaction with vernalization on the processes of flowering.

The induction of florescence should be interpreted as the "chain" of processes (Doorenbos and Wellensiek 1953), owing to which the plant becomes ripe for flowering in the sense of Klebs. It is also more correct to interprete the further development of generative organs as the series of processes on which exterior conditions exert a regulating effect ranging from distinct stimulation to distinct inhibition for the different phases of this process.

If we assume that *P. supina* is actually a photoperiodically neutral plant as regards generative induction, then the differences observed in generative development would concern the second period of this photosensitive process comprising the development of stems and of the flower organs on them.

These processes occur most quickly and intensively under long or continuous light interacting with what is considered by us as optimum light conditions. The accumulation of activators or stimulators of generative development is in these conditions most intensive.

On the other hand the slowed down process of this accumulation under long or continuous illumination in non-optimal light conditions can be intensified by the action of lowered temperature resulting in a speeding up of flowering in comparison to the control combinations.

Under short day, development of stem and florescence were only observed upon vernalization, and this indicates that the inhibition of the process of accumulation of the "development activator" is abolished by the action of lower temperatures. It is assumed in numerous works dealing with the period of dormancy that the inhibitors arising under the influence of short day decompose subsequently under the action of low temperature. The inhibitory effect of "long night" on the development of long-day plants is sometimes also interpreted as due to the formation of inhibitors.

Eaglers and Wareing (1963) believe, on the basis of their investigations on the dormancy period of tress, that the activating effect of lower temperature should not be explained by the decomposition of inhibitors, but rather by the influence of these factors enhancing the synthesis of endogenic gibberellins.

In analogy to the effect of vernalization under long day and to the difference in development under the same daylength but at various light intensities, it would perhaps be more correct to assume that the synthesis of the stimulator occurs also under short day, however it is so slow that the accumulation does not reach the "minimum threshold" or attains it but seldom and after a very long time, thus the lower temperature would act under these conditions only as "catalyst" of this process.

The results of the enormous experimental material accumulated to date, interpreted in the light of the "hormonal" theory of flowering would indicate the quantitative character of this process, and on the other hand, the chain character of the synthesis of hormones exhibiting different degrees of stability at the particular stages.

In the diurnal cycle, processes both of synthesis and decomposition would occur and the "generative effect" would depend on the ratio between the quantity of stable "activator" and of that decomposed in the intermediate steps of the process.

Under long day or continuous illumination with higher light intensity the process of accumulation of stable "activators" runs quickest. Under long day in a weaning light conditions decomposition is more intensive therefore accumulation is retarded. Lower temperature activates the process of accumulation, either by slowing down the rate of decomposition or by intensifying the synthesis.

Under short day, owing to the long night period, the processes of decomposition were not compensated by the process of synthesis, hence the inhibition of generative development. The mechanism of action of low temperature under this assumption would have the same character as that suggested above — activating accumulation.

5. The effectiveness of vernalization in the present experiments showed some differences in dependence on the photo-conditions before and after this treatment.

Particularly wide differences occurred between the results obtained in expts. III and IV exhibiting a very strong accelerating effect and exp. V in which the response to vernalization was observed only in short-day combinations.

As regards the influence of long day before vernalization, it was not significant in expt. III, in expt. IV a slight retardation was noted in plants growing under short day before vernalization. In expt. V the effect was rather reverse, the differences being in all cases unimportant so that we may only speak of a "tendency".

In our observations, on *Rumex obtusifolium*, long-day treatment before vernalization strongly inhibited its effect.

In other plants a relation between the effect of vernalization and daylength in its course was observed (A. Markowski 1959; Napp-Zinn 1960, I Mitt.).

Higazy (1962) studied the relation between daylength, light intensity and the effect of vernalization. According to this author, if *Lunaria biennis* was subjected in the period preceding vernalization to light of high intensity, under long day an abbreviated juvenile phase was obtained and the reactivity of the young plants increased, and, reversely, with very low light intensity, the effect of vernalization was reduced or failed to appear. On the other hand in *Arabidopsis* (Napp-Zinn 1960, II Mitt.) florescence occurred earlier, if light intensity was low before, and high after vernalization.

In these conditions earlier coming into flower, thus of younger plants, were also observed.

The effects of light before and during vernalization do not only differ from species to species, but also in dependence on the age of the plants, the seeding date and the interaction between light intensity and daylength, therefore the interpretation of these phenomena meets with difficulties.

6. Wide differences in the effectiveness of vernalization were found between the plants of Expts. III and IV, and those of Expt. V.

This may have been due to various causes in connection with the different seeding dates, thus the different age of the plants and a shorter period of vernalization. The plants of Expt. III were subjected to vernalization 138 days, in Expt. IV, 72 days and in Expt. V, 117 days after sprouting.

No data are available for determining the length of the juvenile, eventually inactive period in *P. supina*. In Expt. IV these plants exhibited an effect of full vernalization. The length of the juvenile phase and the extent of reactivity in the post-juvenile phase may undergo modifications (Junges 1959, Doorenbos and Wellensiek 1959; Higazy 1962), nevertheless, a weaker light intensity in the post-juvenile phase (Napp-Zinn 1960 and some of the author's own observations) has a favourable effect on the perception of the vernalization stimulus.

The vernalization in Expt. V was shorter. The plants of Expts. III and IV were vernalized under natural conditions, and, as seen in Graph 2, only a part of this period lay within the limits of vernalizing temperatures.

In Expt. V vernalization lasted 31 days, the majority of which could be considered as active, thus a period sufficiently long for making it effective. It may, however, be assumed that the shorter period of vernalization reduced in some extent its effectiveness (Graph 4).

These two assumptions of reduced effectiveness of vernalization: owing to its shorter duration and perhaps to the diminished reactivity of the plants due to a prolonged juvenile phase, do not explain, however the reactions observed. In L_{16} and L_{24} plants the reaction failed to occur and in combination S_8, although significant, it was less pronounced than in the previous experiments.

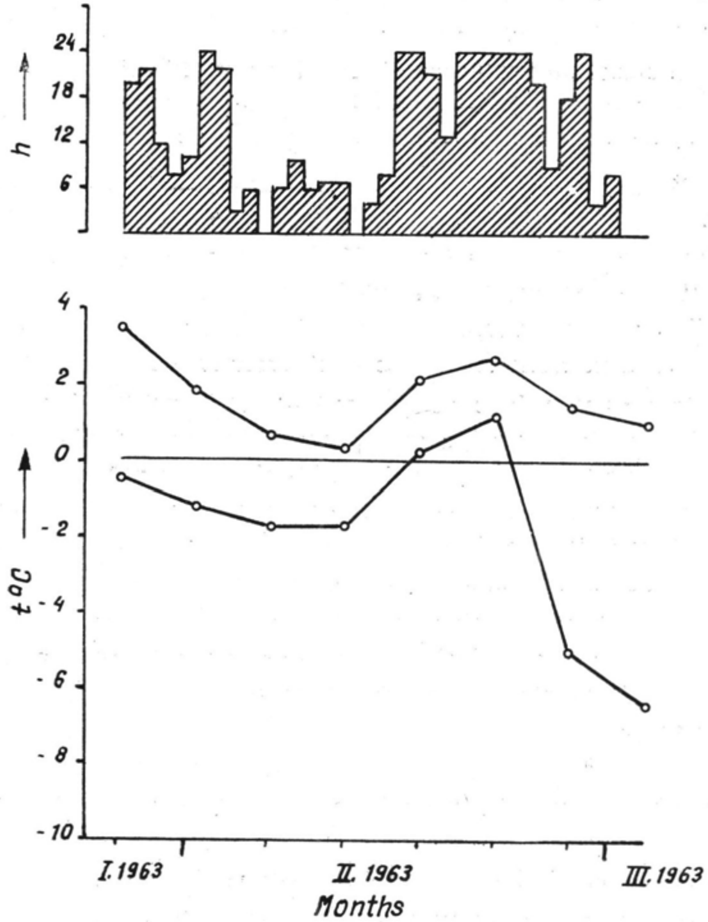
If there had been a lack of perception of the vernalization stimulus or devernalization, then a lack of effectivenes should be expected, in the first place in S_8 plants, whereas the opposite occurred. Therefore some other causes of differences in the reactions of the plants must have been at play.

The plants of Expt. III grew for a longer time under light conditions favourable to growth and photosynthesis and making possible the storage of reserves.

The conditions of development of the plants in Expt. IV were not soo good (hence a lesser speeding up to growth after vernalization as compared to that in Expt. III, see Tables V and VII), nevertheless much more advantageous than in Expt. V.

The plants of Expt. V grew the whole time under light of low intensity, consequently the net-assimilation level must have been lower and the carbohydrate reserves smaller, and these reserves are known to play an important role in the generative development as well as in the process of vernalization (Purvis 1961, Naylor 1961).

An intensive vegetative differentiation and growth started after vernalization in the plants under L_{16} and L_{24} (additionally activated by vernalization). In these conditions there must have occurred a rapid using up of reserves for vegetative development before new leaves developed. Now, in turn, a negative interaction occurred between the young active leaves, thus vegetative development, and the development of shoots and generatives organs (Lange 1961 and references quoted by him, particularly De Zeuw 1956). This resulted in the inhibition of the vernalization stimulus. After transfer to the glasshouse under favourable summer long day conditions the plants bloomed, but, as could be expected, at the same time as the controls (see p. 4 of the present discussion).



Graph. 4. The upper part — the quantity of hours with temperature above 0°C within a day; the lower part — mean temperature max., min.

Under short day — with growth and vegetative development slowed down — these causes had a much weaker effect, therefore the influence of vernalization consisting in differentiation of the shoots and florescence became manifest. The plants came into flower, however, with delay and only partly.

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Rozwój Potentilla supina

Streszczenie

Badano rozwój wegetatywny i generatywny przy różnych terminach siewu na dniu różnej długości — i w interakcji z jaryzacją.

1. Zawiązki pączków zakładające się w kątach liści rozety pierwotnej — rozwijają się w pędy generatywne na dniu ciągłym i długim, a w interakcji z jaryzacją również na krótkim. Główny wierzchołek wzrostu różnicuje się nadal wegetatywnie.

Przy siewie w optymalnych (IV—V miesiąc) warunkach świetlnych — przy wysokim natężeniu światła na dniu długim lub ciągłym — obserwuje się również przejście głównego wierzchołka wzrostu w pęd zakwitający. Roślina w tych warunka staje się monocykliczną.

2. Intensywność wzrostu jak i rozwoju generatywnego — na dniu ciągłym i długim wykazuje wyraźny związek z cyklicznymi zmianami układów świetlnych w skali roku.

Hamujący wpływ wywierany przez krótki dzień, wykazuje natomiast zbliżone nasilenie przy różnych poziomach natężenia światła.

3. Zależność rozwoju od oddziaływania niższych temperatur ma charakter fakultatywny:

Na dniu krótkim — w interakcji z jaryzacją następuje zakwitanie roślin.

Na dniu ciągłym i długim — przy niższych natężeniach światła, jaryzacja występuje jako czynnik przyspieszający wzrost pędów i zakwitania i intensyfikuje sam proces kwitnienia.

4. Przy różnych terminach siewu roślina przechodzi te same fazy przy różnych układach świetlnych. Stąd, w zależności od wieku rośliny i układu warunków zewnętrznych — może być różna reakcja roślin. Stąd też w poszczególnych doświadczeniach obserwowano różną reakcję roślin, a więc i różny wpływ jaryzacji na przyśpieszenie procesów generatywnych.

W ustępie otatnim pracy autor omawia szereg hipotez, mogących pomóc w tłumaczeniu przyczynowym reakcji roślin.